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## LAGOMORPHS (MAMMALIA) FROM LATE MIOCENE DEPOSITS AT LEMUDONG'O, SOUTHERN KENYA

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### ABSTRACT

Remains of 51 fossil Lagomorpha specimens were recovered from late Miocene deposits (ca. 6 Ma) at Lemudong'o, Narok, Kenya. The majority of the fossil remains are postcranial elements and are identified as Leporidae ( $n = 40$ ) based on their morphological characteristics; they represent a minimum of four individuals. Quantitative analysis of the postcranial remains suggests that this assemblage comprises a single population. A maxillary fragment that includes P2 through P4 is tentatively assigned to genus *Alilepus* (Dice, 1931). Taphonomic analysis of this assemblage indicates element preservation is density mediated, but fragmentation is limited and this suggests carnivorous-bird accumulation. The Lemudong'o sample represents the first record of cf. *Alilepus* sp. at this locality and only the second record of *Alilepus*, or a closely allied, genus in Africa (Winkler 2003). These remains confirm an expansion of leporids into the Narok region by ca. 6 Ma.

### Introduction

This paper presents an initial descriptive analysis of 51 lagomorph-fossil skeletal specimens collected from late Miocene (ca. 6 Ma) deposits at the Lemudong'o paleontological site, near Narok, southern Kenya (Ambrose et al., 2003; Ambrose, Kyule, and Hlusko, 2007). In this paper, a specimen is a "bone or tooth, or fragment thereof, from an archaeological or paleontological site, while an element is a single complete bone or tooth in the skeleton of an animal" (Grayson, 1984, p. 16, following Shotwell 1955; Shotwell, 1958). Like other groups of mammals, Lagomorpha "took advantage of the opening of terrestrial connections" to enter Africa during the late Miocene (Lavogat, 1978, p. 84); however, less is known about the early evolutionary history of Lagomorpha (Kingdon, 1974; Lavogat, 1978) than of many other mammalian groups. Thus the results presented here are important to the overall documentation and appreciation of lagomorph evolution in general, and in particular, they contribute to understanding the geographic range of some of the earliest African leporids.

The order Lagomorpha, with only two extant families and 12 extant genera, are herbivorous and have a moderately broad adaptive range. Extant lagomorphs inhabit forested areas, grasslands, deserts, and tundra, a range which most likely characterizes their fossil allies as well. Ochotonidae, or pikas, are more limited in their modern geographic distribution—Holarctic and often high altitude—than are Leporidae, or rabbits and hares, which have become ubiquitous (albeit introduced by humans in the case of Australasia and South America) to all but the West Indies, Madagascar, and Antarctica (see Kingdon, 1974; Nowak, 1991).

First recognized from late Paleocene deposits in northern China and Mongolia, lagomorphs have been relatively stable morphologically, with general evolutionary trends that include simplification of the cheek-tooth pattern, increased hypsodonty, and some gradual, adaptational changes related to locomotion (Dawson, 1967). Although the origin of this order is still under question, recent phylogenetic analysis of character traits on fossil specimens from Mongolia suggest that lagomorphs, along with rodents (collectively known as the superorder Glires), diverged from other placentals within a few million years of the Cretaceous-Tertiary boundary (Ascher et al., 2005). Lagomorpha radiation begins with fossil Leporidae in the late-middle to late Eocene with at least nine different genera represented in the Asian fossil record (see Van Valen, 1964; Meng et al., 2005). The diversity of ochotonids and leporids, expressed by the number of known genera, varies over time, with Ochotonidae appearing in the middle Oligocene, and radiating in the late Oligocene through the Miocene to achieve their greatest variety and geographic distribution—North America and Eurasia. Leporidae, however, increased gradually and eventually overtook ochotonids in variety and range beginning in the late Pliocene (Dawson, 1967; Dawson, 1981).

The earliest Ochotonidae in Africa come from Miocene deposits at Nambib, Namibia (*Australagomys* Stromer, 1926) and from Rusinga Island, Kenya (*Kenyalagomys* MacInnes, 1953), with these latter materials dating to the early Miocene, around 18 Ma (Van Couvering and Miller, 1969). Although the ochotonid *Prolagus* is reported from late Miocene-late Pliocene deposits of North Africa (Benammi et al., 1996), by the end of the

Miocene Ochotonidae are entirely replaced by Leporidae in sub-Saharan Africa.

Fossil evidence indicates that Leporinae likely originated from Archaeolaginae (which likely descended from Oligocene Palaeolaginae) in North America sometime in the middle to late Miocene (White, 1991). Leporids in the form of *Alilepus* (Schlosser, 1924) and *Hypolagus* (Dice, 1917) first appear in northeastern Asia around 8 Ma. Recent research, based on morphological and mtDNA evidence, suggests at least three intercontinental exchanges occurred between North American and Asian leporids during the Miocene, and most likely an additional three dispersals of leporids occurred from Eurasia into Africa (Matthee et al., 2004). By the Mio-Pliocene boundary genera such as *Pliopentalagus*, *Trischizolagus*, and *Serengetilagus* derive from an *Alilepus*-like population with *Pliopentalagus* and *Trischizolagus* spreading across Eurasia and giving rise to various extant Old World genera, and *Serengetilagus* spreading into Africa (Patnaik, 2002, p. 449). *Serengetilagus* disappears after the early Pleistocene, with *Lepus* (ubiquitous) and *Pronolagus* (southern Kenya to the Cape of Good Hope) emerging in the middle to late Pleistocene (Dawson, 1957; Kingdon, 1974). *Oryctolagus* is a recent Holocene arrival to northwestern Africa from southern Europe (Kingdon, 1974).

Modern Leporidae comprise rabbits and hares that presently inhabit forests, shrub areas, grasslands, tundra, and alpine slopes, and feed on a variety of plants. Taxonomic controversies over the extant genus *Lepus*, and in particular the Old World *Lepus*, are largely due to the fact that interspecific variation in qualitative and quantitative morphological characteristics is small compared to intraspecific geographic and individual differences (Angermann, 1983). This detail makes the identification of skeletal leporid remains below the family level somewhat problematic.

### Materials and Methods

At Lemudong'o Locality 1, 40 lagomorph specimens were amassed over five separate field seasons by intensive surface collection of this locality in 1995, and between 2000 and 2004 (Ambrose, Kyule, and Hlusko, 2007). In addition, 11 specimens (KNM-NK 41457) were recovered from geological deposits at Enamankeon in 2001 using similar recovery techniques. Both localities are demonstrated to be of a similar depositional environment and are contemporaneous (Ambrose, Nyamai, et al., 2007). Field sorting and specimen photography was undertaken by L. Hlusko; casts of the specimens were prepared in Nairobi by L. Hlusko at the National Museums of Kenya, Division of Casting. The original specimens are curated with the Division of Palaeontology, National Museums of Kenya, under the prefix KNM-NK. Specimen casts are housed in the Department of Integrative Biology at the University of California, Berkeley. For the purpose of this analysis all Lagomorpha specimens are considered to be a single sample. KNM-NK 42368, a maxillary cheektooth recovered in 2002 from modern silts, is excluded from the total specimen count and analysis.

The majority of the specimens described here are postcranial (84%), and with the exception of one maxillary fragment, the cranial specimens are limited to isolated teeth. The emphasis for this analysis, therefore, is on the postcrania. Casts and photographs of the Lemudong'o postcranial specimens were compared with African leporid postcrania in the Department of Mammalogy at the Smithsonian Institution's National Museum of Natural History. This is probably the largest collection of African leporids in North America with 646 individuals, but only six of these have postcranial elements. (By comparison, the Museum of Vertebrate

Zoology at the University of California, Berkeley, houses 33 specimens of African leporids, but none have postcranial skeletal elements.) The fossil specimens were also compared with western North American leporid postcrania from the Zooarchaeology Laboratory, University of California, Davis. Fossil and extant specimens were measured with digital metric calipers to the nearest tenth of a millimeter following standards set by von den Driesch (1976). Dental abbreviations follow Smith and Dodson (2003).

### Systematic Paleontology

Class MAMMALIA Linnaeus, 1758

Order LAGOMORPHA Brandt, 1855

Family indeterminate

### Material

KNM-NK 40901, phalanx, fragment; KNM-NK 40997, tooth, fragment; KNM-NK 41254, incisor, fragment; KNM-NK 42249, proximal/middle phalanx, distal end; KNM-NK 42317, proximal/middle phalanx, distal end; KNM-NK 44812, incisor, fragment.

### Remarks

A total of six specimens were recovered, which comprise broken phalanges, and incisor or cheektooth fragments. With the exception of the two fragmentary incisors, the specimens were field identified but not photographed or cast. Given their fragmentary state these elements could not be confidently identified to a lower taxonomic level than order Lagomorpha.

Family LEPORIDAE (Fischer de Waldheim, 1817) Gray, 1821

### Remarks

The family Leporidae was first defined in a French publication by German paleontologist Fischer de Waldheim in 1817, who was professor of Natural History at Moscow University, but Leporidae was also later defined in an English publication by Gray in 1821 (McKenna and Bell, 1997); both are typically cited for this family. The vast majority of the lagomorph-fossil specimens recovered from Lemudong'o were identified to family Leporidae; these remains are composed of postcranial elements ( $n = 40$ ) and isolated teeth ( $n = 4$ ).

In the Tugen Hills sequence of the Kenyan Rift Valley, the first leporids appear in the Mpesida Beds after a substantial gap in this sequence between about 8.5 and 6.5 Ma, and they continue to be represented in the subsequent Lukeino Formation (ca. 6.2 to 5.6 Ma) (Hill, 1999, p. 90). These leporids are represented by only three isolated tooth specimens—an incisor from the Mpesida Beds, and a cheektooth and premolar from the Lukeino Formation (Winkler, 2002, p. 240), the latter of which (LP3) may be attributable to *Alilepus* (Winkler, 2003, p. 171). Winkler (2002, p. 250) further suggests that the Lukeino leporid is congeneric with comparable-aged leporids from the Siwaliks, Pakistan, which implies interchange between these two areas.

From the lower Nawata Formation, at the site of Lothagam, in the Turkana desert region of northern Kenya, another early record of Leporidae is represented by cranial and postcranial remains of at least two individuals, which have been assigned to *Alilepus* and dated to 6.57–6.54 Ma (Winkler, 2003, p. 170). Only the p3 specimens are illustrated and described. Later Pliocene specimens of the leporid *Serengetilagus* have been identified from Lake Eyasi in Tanzania (MacInnes, 1953), from Kossom Bougoudi in northern Chad (Brunet et al., 2000), and most





**Figure 1.** KNM-NK 41457, Leporidae specimens recovered from Enamankeon; tibia, calcaneus, astragalus, cuboid, metatarsals, proximal phalanges (hindlimb).

recently from the Apak Member (ca. 4.2 Ma) of Lothagam (Winkler, 2003).

Family LEPORIDAE (Fischer de Waldheim, 1817) Gray, 1821

Genera and species indeterminate

Figure 1

### Material

KNM-NK 36961, L. tibia, distal end; KNM-NK 36962, R. calcaneus, tuber calcus; KNM-NK 40876, R. and L. humerus (distal end), R. and L. radius (proximal end); KNM-NK 40895, L. calcaneus; KNM-NK 40917, L. ilium, caudal 1/2 and acetabulum; KNM-NK 40991, R. tibia, distal end and 1/4 shaft; KNM-NK 41001, R. tibia (distal end and 1/4 shaft), navicular; KNM-NK 41003, L. femur, proximal end and 1/4 shaft; KNM-NK 41025, R. tibia, distal end; KNM-NK 41065, proximal hindlimb phalanx; KNM-NK 41078, maxillary cheek tooth; KNM-NK 41323, R. astragalus, L. astragalus; KNM-NK 41457, R. tibia, R. astragalus and calcaneus, L. cuboid, R. metatarsal I, R. metatarsal III, L. metatarsal IV (proximal end and 1/4 shaft), metatarsal (distal end and 1/3 shaft), metapodial (midshaft fragment), two proximal hindlimb phalanges; KNM-NK 41478, L. calcaneus, tuber calcus; KNM-NK 41486, L. femur, caput femoris; KNM-NK 41493, metapodial, distal end and 1/4 shaft; KNM-NK 42253, L. cuboid; KNM-NK 42265, R. astragalus; KNM-NK 42290, calcaneus, tuber calcus; KNM-NK 42292, maxillary cheek tooth; KNM-NK 42299, L. LP3; KNM-NK 42307, R. humerus, distal end; KNM-NK 42356, R. astragalus, condyle fragment; KNM-NK 44763, L. humerus, distal end; KNM-NK 44772, L. femur, distal end; KNM-NK 44773, L. femur, distal end; KNM-NK 44813, middle phalanx, distal and 1/2 shaft; KNM-NK 44824, proximal phalanx, distal and 1/2 shaft; KNM-NK 45801, mandibular cheek tooth.

### Descriptions and remarks

A total of four isolated teeth from Lemudong'o were identified as leporid. KNM-NK 42299 is an isolated left mandibular third

premolar, which has a mesio-distal dimension of 3.3 mm and a buccal-lingual dimension of 2.9 mm. Although the tooth compares favorably to the general characteristics of a leporid p3, the occlusal surface has postmortem wear and edge chipping which makes further identification difficult. Among Leporidae the occlusal or enamel patterns of maxillary (post P2) and mandibular (post p3) cheek teeth exhibit little variation. The maxillary (KNM-NK 41078 and 42292) and mandibular (KNM-NK 45801) cheek tooth specimens from Lemudong'o are no exception and follow the general leporid pattern.

An additional 40 postcranial elements were assigned to family Leporidae, and measurements of these remains are presented in Table 1. Four humeri were recovered and all of the fragments are the distal end with no remains of the shaft. A left distal end fragment from two different individuals (KNM-NK 40876 and 44763) and a right distal end fragment (KNM-NK 42307) are quite eroded on the margins and the fragments do not extend to the olecranon foramen (supratrochlear fenestra) but they resemble *Lepus*. The other right distal end fragment (KNM-NK 40876) extends to just past the olecranon foramen, which is a characteristic trait of leporids. However, this fenestra is quite wide and more prominent than found in modern leporids and is more similar to descriptions for *Palaeolagus* (Scott et al., 1940), which suggests that the elbow joint of this fossil leporid might have had more flexibility than its modern counterpart. Only the proximal end of a right and left radius were preserved (KNM-NK 40876), both compare favorably with general leporid radial head and neck morphology.

The ilium, KNM-NK 40917, which includes the acetabulum, the anterior inferior spine and the caudal portion of the iliac blade, is basically similar to the general leporid innominate, albeit the acetabular rim has a less prominent margin than *Lepus* and is more similar in this characteristic to *Sylvilagus*.

The largest femoral fragment is KNM-NK 41003, a left anterior surface of the proximal end with an unfused head (caput femoris). The first trochanter of the greater trochanter is missing, and the edges of the anteriolateral margin of the third trochanter are worn. Although in overall appearance it compares favorably

**Table 1.** Postcranial element measurements (in mm) of Lemudong'o Leporidae (KNM-NK) specimens. GL = greatest length, GB = greatest breadth, Bp = breadth proximal, Bd = breadth distal, Dd = depth distal, SD = smallest breadth diaphysis, DC = depth caput, LAR = length of acetabulum at rim (von den Driesch, 1976).

KNM-NK no.	Skeletal Element	GL	GB	Bp	Bd	Dd	SD	DC	LAR
41323	Astragalus (R.)	12.5	—	—	—	—	—	—	—
41323	Astragalus (L.)	12.4	—	—	—	—	—	—	—
41457	Astragalus (R.)	13.1	—	—	—	—	—	—	—
40895	Calcaneus (L.)	24.1	7.4	—	—	—	—	—	—
41457	Calcaneus (R.)	27.4	8.4	—	—	—	—	—	—
41457	Cuboid (L.)	9.7	—	—	—	—	—	—	—
42253	Cuboid (L.)	9.2	—	—	—	—	—	—	—
41486	Femur (L.)	—	—	—	—	—	—	7.8	—
44772	Femur (L.)	—	—	—	13.5	—	—	—	—
44773	Femur (L.)	—	—	—	13.8	—	—	—	—
40876	Humerus (R.)	—	—	—	13.4	—	—	—	—
40876	Humerus (L.)	—	—	—	13.5	—	—	—	—
41457	Metatarsal I (R.)	43.7	—	—	5.8	—	—	—	—
41457	Metatarsal III (R.)	47.1	—	—	4.7	—	—	—	—
41001	Navicular	—	8.1	—	—	—	—	—	—
40917	Ilium (L.)	—	—	—	—	—	—	—	9.7
41457	Proximal phalanx, hindlimb	17.6	—	5.1	4.8	—	3.2	—	—
41457	Proximal phalanx, hindlimb	17.5	—	5.2	4.7	—	3.3	—	—
40876	Radius (R.)	—	—	9.1	—	—	—	—	—
40876	Radius (L.)	—	—	8.5	—	—	—	—	—
36961	Tibia (L.)	—	—	—	12.1	8.0	—	—	—
40991	Tibia (R.)	—	—	—	12.4	7.2	—	—	—
41001	Tibia (R.)	—	—	—	12.3	7.0	—	—	—
41025	Tibia (R.)	—	—	—	12.8	7.2	—	—	—
41457	Tibia (R.)	123.8	—	—	—	8.1	7.1	—	—

with leporids in general, the third trochanter is more similar to *Trischizolagus* (Averianov, 1995, p. 381–382) and *Sylvalagus*, than to *Lepus*, as the crest is less developed. Since this is a juvenile femur, the lack of crest development could be due to age and reduced muscle development; however, the trochanters are more developed than on *Palaeolagus* (Dice, 1932; Scott et al., 1940). KNM-NK 41486 consists only of a left femoral head; KNM-NK 44772 comprises the distal condyles of a left femur with a faint fusion line, and 44773 is also a left distal end but it is completely fused. All are well within the norm for leporids.

A complete tibia was recovered in three fragments that were refit (KNM-NK 41457), and it is remarkably similar both to modern and fossil leporids (e.g., *Trischizolagus* [Averianov, 1995, p. 381–382]) in morphological characteristics. This specimen has a greatest length (GL) of 123.8 mm (Figure 1), which is well within the range of modern jack-rabbits and cape hares (*Lepus* spp.). Complete tibiae are rare in the fossil record, but by comparison, an Oligocene-aged *Palaeolagus* is reported to be 56.3 mm (Dice, 1932, p. 303), which is considerably smaller. The other tibiae recovered from Lemudong'o are right and left distal ends, and right distal ends with one quarter of the distal shaft, and they derive from the same population as the above described complete tibia.

A total of five astragali, five calcanei, two cuboids, one navicular, metatarsal I, III, and IV, two metatarsal fragments, one metapodial fragment, three hindlimb proximal phalanges, and a proximal and middle phalanx were recovered from Lemudong'o. These hindfoot (pes) elements represent a minimum of four individuals. KNM-NK 41323 are complete right and left astragali, 41457 (Figure 1) and 42265 are complete right astragali with slight erosion on the bony margins, and 42356 is an articular condyle fragment. The astragalonavicular articular facet is narrower and extends more posteriorly than in *Palaeolagus*

(Szalay, 1985, p. 118) and *Lepus* and is more similar in width to *Trischizolagus* (Averianov, 1995, p. 381) and *Sylvalagus*. However, this facet forms a somewhat elongated point in the Lemudong'o specimens. The shape of the sustentacular and the overall proportions are the same as other leporids.

The lagomorph calcaneus of *Palaeolagus* has been well described by Szalay (1985) and the presence of an enlarged calcaneal canal in fossil lagomorphs (Leporidae: *Palaeolagus* and *Hypolagus*) has been noted by Bleefeld and Bock (2002). Like *Palaeolagus* and *Hypolagus* (Bleefeld and Bock, 2002) the calcaneal canal is quite prominent in the Lemudong'o specimens (KNM-NK 40895 and 41457, Figure 1), whereas this canal is small and sometimes absent in modern *Pronolagus*, *Oryctolagus*, *Lepus*, and *Sylvalagus*. The proximal calcaneo-astragalar facet has a distinctive transverse ridge dividing it into two parts, which is considerably different from the smoother, sloped appearance of *Palaeolagus* (Szalay, 1985, p. 117). This ridge is found in modern leporids and is reported for *Trischizolagus* (Averianov, 1995, p. 382).

Both the cuboid and navicular are the same as modern Leporidae. The metatarsal shafts are slightly stockier than the long, slender appearance of *Lepus*, but not as short, proportionally, as *Palaeolagus* (Scott et al., 1940) and are more similar to *Trischizolagus* (Averianov, 1995), but in every other respect (i.e., articular facets) the specimens do not differ from *Palaeolagus*, *Hypolagus*, *Trischizolagus*, or modern leporids. The phalanges are identical to those of other fossil and extant leporids.

Since the distal tibia is the most commonly occurring element portion in the Lemudong'o fossil-leporid assemblage, further comparison with extant African and North American leporid tibiae was undertaken (Table 2, Figure 2). The smallest distal tibiae in this sample are the western North American desert (*Sylvalagus audubonii*) and Nuttall's cottontails (*Sylvalagus nuttali*)

**Table 2.** Distal tibiae measurements (in mm) of Lemudong'o Leporidae (KNM-NK) compared to modern African (SI) and North American (UCD) Leporidae. Bd = Breadth distal; Dd = Depth distal (von den Driesch, 1976).

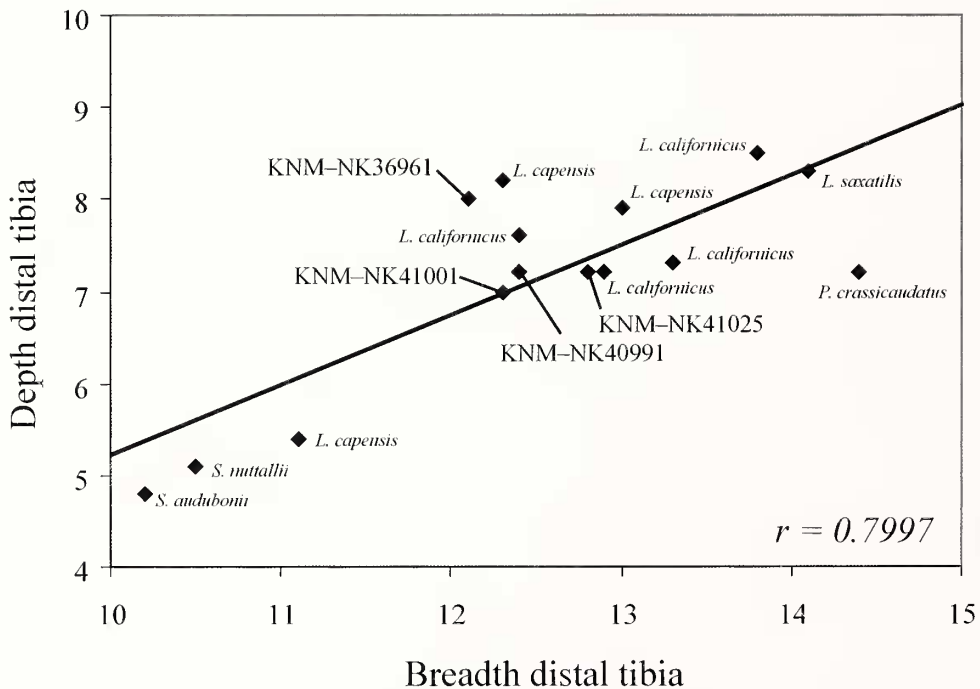
Taxa	Tibia Specimen No.	Bd	Dd
<i>Sylvilagus audubonii</i> (Audubon/desert cottontail)	UCD 1011	10.2	4.8
<i>Sylvilagus nuttallii</i> (Nuttall's cottontail)	UCD 1169	10.5	5.1
<i>Lepus capensis</i> (cape hare)	SI 326766	11.1	5.4
Leporidae	KNM-NK 36961	12.1	8.0
Leporidae	KNM-NK 41001	12.3	7.0
<i>Lepus capensis</i> (cape hare)	SI 341059	12.3	8.2
Leporidae	KNM-NK 40991	12.4	7.2
<i>Lepus californicus</i> (black-tailed jack rabbit)	UCD 1168	12.4	7.6
Leporidae	KNM-NK 41025	12.8	7.2
<i>Lepus californicus</i> (black-tailed jack rabbit)	UCD 1161	12.9	7.2
<i>Lepus capensis</i> (cape hare)	SI 18818	13.0	7.9
<i>Lepus californicus</i> (black-tailed jack rabbit)	UCD 1368	13.3	7.3
<i>Lepus californicus</i> (black-tailed jack rabbit)	UCD 1016	13.8	8.5
<i>Lepus saxatilis</i> (scrub hare)	SI 221372	14.1	8.3
<i>Pronolagus crassicaudatus</i> (Natal's red rock hare)	SI 22972	14.4	7.2
	<b>Average</b>	<b>12.5</b>	<b>7.1</b>
	<b>Minimum</b>	<b>10.2</b>	<b>4.8</b>
	<b>Maximum</b>	<b>14.4</b>	<b>8.5</b>
	<b>Standard Deviation</b>	<b>1.2</b>	<b>1.7</b>

l*ii*), which are more than a millimeter narrower in distal breadth, and nearly three millimeters narrower in distal depth, than any of the Lemudong'o specimens. At the other extreme, the distal tibia specimens of the African scrub hare (*Lepus saxatilis*) and African red rock hare (*Pronolagus crassicaudatus*) are minimally two-millimeters wider in distal breadth but equivalent in distal depth to the Lemudong'o specimens. The distal tibiae from Lemudong'o overlap, albeit on the smaller end, with those of both the African cape hare (*Lepus capensis*) and the North American black-tailed jackrabbit (*Lepus californicus*).

Family LEPORIDAE Gray, 1821  
Genus ALILEPUS Dice, 1931

**Remarks**

The genus *Alilepus* was first defined by Dice (1929, p. 342; 1931, p. 159) and assigned to the family Leporidae (McKenna and Bell, 1997). The type specimen, which was found in Mongolia, was originally described as *Lepus [Alilepus] amnectus* (Schlosser 1924, p. 44). Further, description of this genus was emended by White (1991, p. 69) based on his analysis of late



**Figure 2.** Scatterplot comparing distal breadth of tibia to distal depth of tibia (in mm) for the Lemudong'o specimens and other leporid species. Specimens and their corresponding measurements from Table 1.



Miocene to Pliocene North American Leporinae specimens. The morphology of the LP3 in particular and to a lesser degree the UP2 was determined to be the most useful for identifying leporines (White, 1991, p. 67; see also Hibbard, 1963; Voorhies and Timperley, 1997).

The earliest *Alilepus* fossils were recovered from late Miocene deposits in northern China (Qui et al., 1985; see also Schlosser, 1924), and have a distribution in Eurasia from the late Miocene to early Pliocene. In North America various species of the genus *Alilepus* have been identified from Miocene deposits across the Great Plains and the Southwest (see White, 1991 for a summary; also Voorhies and Timperley, 1997), and this genus has been identified from late Miocene deposits, Lower Nawata Formation, Lothagam, Kenya (Winkler, 2003).

Genus cf. *ALILEPUS* Dice, 1931

Figure 3, 4A

### Material

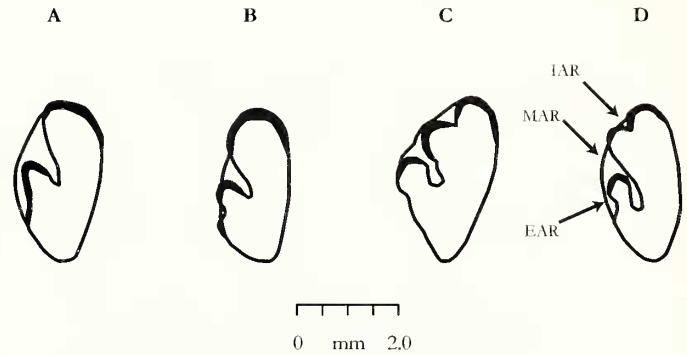
KNM-NK 36939, R. maxillary fragment with UP2–P4.

### Description and remarks

KNM-NK 36939 is fragmentary specimen of the right maxilla comprising P2–4 and only the palate and alveolar bone surrounding the teeth (Figure 3). The P2 has a buccal-lingual length of 3.2 mm and a mesial-distal width of 2.0 mm. It has a deeply incised main anterior reentrant (MAR) that extends nearly halfway across the tooth, a very shallow external anterior reentrant (EAR), and no internal anterior reentrant (IAR) (Figure 4). The other two premolars are typical of leporids; they are both bilobate and oval-shaped in occlusal view with a slight ridge separating the higher mesial lobe from the lower distal lobe. The P3 has a buccal-lingual length of 4.7 mm and a mesial-distal width of 2.1 mm, and the P4 has a buccal-lingual length of 4.7 mm and a mesial-distal width of 2.2 mm. Although association with a p3 is preferred for identification to genus (Dawson, 1967), KNM-NK 36939 is tentatively assigned to *Alilepus* based on visual assessment of the P2 cast and photographs following criteria established by White (1991).



**Figure 3.** Occlusal view of KNM-NK 36939, cf. *Alilepus*, a right maxillary fragment with P2–4. Buccal is to the top of the photograph. The P2 has a buccal-lingual width of 3.2 mm and a mesio-distal length of 2.0 mm.



**Figure 4.** Occlusal view of Leporidae P2's: A = cf. *Alilepus* (KNM-NK 36939) from Lemudong'o; B = *Alilepus hibbardi* (White 1991, p. 73, fig. 6); C = *Serengetilagus praecapensis* (MacInnes 1953, p. 28, fig. 16); D = *Lepus capensis* (MacInnes 1953, p. 28, fig. 17). Location of main anterior reentrant (MAR), external anterior reentrant (EAR), and internal anterior reentrant (IAR) are noted on D.

### Taphonomic Analysis

Of the 51 fossil specimens identified to the order Lagomorpha, 45 are assigned to the family Leporidae, representing a minimum of four individuals. Minimum number estimates are based on the recovery of four distal right tibiae and four right astragali (Table 3). The Enamankeon specimens comprise only 28.2% of the total leporid assemblage with an NISP of 11 and an MNI of one, and they derive only from the lower hind-limb portion: one tibia, three tarsals, five metatarsals, and two phalanges. Conversely, the leporid remains from Lemudong'o Locality 1 are represented by portions of front and hind limbs, the pelvis, and the maxilla.

To assess the extent of post-depositional bone attrition at this locality, the ratio of NISP:MNE and the average relative frequency of complete skeletal elements was used to gauge the extent of fragmentation (following Lyman, 1994). The results reveal that fragmentation of this assemblage is limited; this outcome likely is driven both by the high percentage of compact tarsal bones (33.3%) relative to other skeletal elements and by small sample size.

The postcranial remains were compared with published volume density values for leporid skeletal elements in order to assess the extent to which the Lemudong'o assemblage is density mediated (Table 4). Pavao and Stahl (1999) computed volume density values for Leporidae in two ways to account for the small size of their skeletal elements: 1)  $VD_{LD/BT}$ , or standard volume density, and 2)  $VD_{SA}$ , or shape-adjusted volume density. Standard volume density is bone mineral density divided by bone volume (normed to a square or rectangular shape); whereas, shape-adjusted volume density calculates bone volume using a more precise estimate of the cross-sectional geometry of the skeletal element. Using a Spearman's rank-order correlation coefficient, the normed relative frequency of leporid minimal animal units is compared with volume density values. The results of this analysis indicate a positive and significant correlation with standard volume density ( $r_s = 0.66$ ,  $P = 0.05$ ), and a positive but insignificant correlation with shape-adjusted volume density ( $r_s = 0.52$ ,  $P = 0.15$ ). Thus, overall the Lemudong'o assemblage is skewed toward denser skeletal elements, which accounts for the high frequency of tarsal bones and the low frequency of crania

**Table 3.** Frequency of Leporidae postcranial skeletal elements from Lemudong'o (Locality 1) and Enamankeon (Locality 1). Terms follow Lyman (1994): NISP = number of identified specimens; MNE = minimum number of complete skeletal elements necessary to account for all observed specimens; N whole = absolute frequency of whole or complete skeletal elements; percent whole =  $100 (\Sigma N \text{ whole} / \Sigma \text{ NISP})$ .

Element	NISP	N Whole	MNE	NISP:MNE	%Whole
Astragalus	5	4	5	1.00	80.0
Calcaneus	5	2	5	1.00	40.0
Cuboid	2	2	2	0.00	100.0
Femur	4	0	2	2.00	0.0
Humerus	4	0	4	1.00	0.0
Ilium	1	0	1	1.00	0.0
Metapodial	2	0	2	1.00	0.0
Metatarsal	1	0	1	1.00	0.0
Metatarsal I	1	1	1	0.00	100.0
Metatarsal III	1	1	1	0.00	100.0
Metatarsal IV	1	0	1	0.00	0.0
Navicular	1	1	1	0.00	100.0
Phalanx, proximal, hindlimb	2	2	2	0.00	100.0
Phalanx, proximal	1	0	1	1.00	0.0
Phalanx, middle	1	0	1	0.00	0.0
Radius	2	0	2	1.00	0.0
Tibia	5	1	5	1.00	20.0
<b>Total</b>	<b>39</b>	<b>14</b>	<b>37</b>		
<b>Average</b>				<b>1.05</b>	<b>35.8</b>

and mandibles (except for isolated teeth). This pattern is similar to reported raptor-pellet accumulations (e.g., Terry, 2004).

### Discussion

The fossil remains from Lemudong'o represent a relatively large sample of Lagomorpha—6% of entire vertebrate assemblage (Ambrose, Bell, et al., 2007)—and specifically leporid specimens from the late Miocene of Africa. Even though the leporid assemblage appears to be driven by density-mediated attrition, generally the fossil remains are well preserved and the elements are relatively complete. Of the 43 postcranial specimens in the Lemudong'o assemblage, 40 are identified to Leporidae with a minimum of four individuals represented. An additional eight cranial fragments were recovered, four of which are identified as leporid and one tentatively as *Alilepus* (P2–4). By comparison, the leporid (*Alilepus*) remains recovered from slightly older late Miocene (Lower Nawata) deposits at Lothagam comprise 14 postcranial and seven cranial specimens, and represent a minimum of two individuals (Winkler, 2003, p. 170).

A single maxillary fragment (P2–4) recovered from Lemudong'o compared most favorably with descriptions of the genus *Alilepus*. As illustrated in Figure 4, KNM-NK 36939 compares most favorably with published descriptions and diagrams of late Miocene *Alilepus* (Schlosser, 1924; White, 1991, p. 73) rather than the early Pliocene-Pleistocene African leporid *Serengetilagus* (Detrich, 1942; MacInnes, 1953, p. 28; Winkler, 2003, p. 172); however, it does resemble some illustrations of *Trischizolagus* (Averianov and Tesakov, 1997, p. 148), which has been identified from late Miocene-Pleistocene Eurasian deposits and may be one and the same with *Serengetilagus* (see Winkler, 2003, p. 171). Both of these genera likely derive from the "Alilepus" pattern, which supports the identification of the Lemudong'o specimen as *Alilepus* species indeterminate.

One problem with the use of a P2 is its high degree of variability both morphologically and in terms of size. Averianov and Tesakov (1997, p. 147) have suggested that smaller P2's with only 1–2 grooves may come from younger animals, whereas larger P2's with three grooves are most likely from older individuals. *Trischizolagus dumitrescuae* from Ruscinian (early Pliocene)

**Table 4.** The minimal animal unit (MAU) is scaled for the number of specific skeletal elements in a rabbit and %MAU are these values normed against the most commonly occurring skeletal element. Volume density values for rabbit skeletal elements are based on analysis by Pavao and Stahl (1999). LD/BT = linear density or bone mineral density/scan site volume (i.e., standard volume density); SA = shape-adjusted volume density. Nonparametric or rank-ordinal statistic, Spearman's rho ( $r_s$ ) used to compare %MAU to density values.

Element	MNE	MAU	%MAU	Density (LD/BT)	Density (SA)
Astragalus	5	2.5	100.0	0.07	0.24
Calcaneus	5	2.5	100.0	0.11	0.26
Femur	2	1.0	40.0	0.08	0.28
Humerus	4	2.0	80.0	0.10	0.37
Ilium	1	0.5	20.0	0.07	0.39
Metatarsal	3	0.3	12.0	0.04	0.13
Phalanx	4	0.1	3.2	0.03	0.03
Radius	2	1.0	40.0	0.07	0.16
Tibia	5	2.5	100.0	0.07	0.43
				$r_s = 0.66$	$r_s = 0.52$
				$P = 0.05$	$P = 0.15$



deposits in Moldova and the Ukraine show a gradual shift from the "*Hypolagus*" pattern toward the dominant "*Alilepus*" pattern (Averianov and Tesakov, 1997, p. 148, Fig. 3a–u). Occlusal-surface illustrations of younger P2 from these Eurasian deposits show a high degree of similarity with KNM-NK 36939, which reinforces the cf. *Alilepus* moniker. Recovery of KNM-NK 36939 from ca. 6 Ma sediments at Lemudong'o (Ambrose et al., 2003) makes this the first occurrence of cf. *Alilepus* in southern Kenya and is one of only two reported occurrences of this genus in Africa, the other being the late Miocene Lower Nawata Formation, at Lothagam in northern Kenya (Winkler, 2002, 2003).

Association of postcranial elements with the cf. *Alilepus* sp. maxillary fragment, and given the lack of morphological variation within the Lemudong'o postcranial leporid assemblage suggests that the postcrania could also be *Alilepus*. The overall morphology of the postcrania is well within the range of fossil and modern Leporidae. Both primitive (e.g., calcaneal canal, wide olecranon foramen) and derived (e.g., proximal calcaneostragalar ridge) characteristics are identified on the postcranial elements, which suggests a transition between archaeolagine and leporine morphology.

The leporids from Lemudong'o are larger than modern cottontail rabbits, smaller than scrub hares and rock hares, and roughly the size of small black-tailed jackrabbits (hares) or mid-sized cape hares. Evaluation of the size of the Lemudong'o fossils to a sample of modern leporids (Figure 2) is not meant to discern any phylogenetic or taxonomic relationships; it does, however, illustrate their relative size. In addition, the Lemudong'o leporids are considerably larger than paleolagines (e.g., Dice, 1932). Since leporids currently occupy both open and forested environments, and because these small mammals could have been transported to the site by carnivorous mammals or birds of prey, it is difficult to determine the late Miocene environment of Lemudong'o based solely on their remains. However, what these fossils do demonstrate is that leporids had expanded in the late Miocene into the Narok region of southern Kenya by at least ca. 6 Ma.

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### References

- Ambrose, S. H., C. J. Bell, R. L. Bernor, J.-R. Boisserie, C. M. Darwent, D. Degusta, A. Deino, N. Garcia, Y. Haile-Selassie, J. J. Head, F. C. Howell, M. D. Kyule, F. K. Manthi, E. M. Mathu, C. M. Nyamai, H. Saegusa, T. A. Stidham, M. A. J. Williams, and L. J. Hlusko. 2007. The paleoecology and paleogeographic context of Lemudong'o Locality 1, a late Miocene terrestrial fossil site in southern Kenya. *Kirtlandia*, 56:38–52.
- Ambrose, S. H., L. J. Hlusko, D. Kyule, A. Deino, and M. Williams. 2003. Lemudong'o: a new 6 Ma palaeontological site near Narok, Kenya Rift Valley. *Journal of Human Evolution*, 44:737–742.
- Ambrose, S. H., M. D. Kyule, and L. J. Hlusko. 2007. History of palaeontological research in the Narok District of Kenya. *Kirtlandia*, 56:1–37.
- Ambrose, S. H., C. M. Nyamai, E. M. Mathu, and M. A. J. Williams. 2007. Geology, geochemistry, and stratigraphy of the Lemudong'o Formation, Kenya Rift Valley. *Kirtlandia*, 56:53–64.
- Angermann, R. 1983. The taxonomy of Old World *Lepus*. *Acta Zoologica Fennica*, 174:17–21.
- Asher, R. J., J. Meng, J. R. Wible, M. C. McKenna, G. W. Rougier, D. Dashzeveg, and M. J. Novacek. 2005. Stem Lagomorpha and the antiquity of Glires. *Science*, 307:1091–1094.
- Averianov, A. O. 1995. Osteology and adaptations of the early Pliocene rabbit *Trischizolagus dumitrescuae* (Lagomorpha: Leporidae). *Journal of Vertebrate Paleontology*, 15:375–386.
- Averianov, A. O., and A. S. Tesakov. 1997. Evolutionary trends in Mio-Pliocene Leporinae, based on *Trischizolagus* (Mammalia, Lagomorpha). *Palaeontologische Zeitschrift*, 71:145–153.
- Benammi, M., B. Orth, M. Viany-Liaud, Y. Chaimance, V. Suteethorn, G. Feraud, J. Hernandez, and J.-J. Jaeger. 1995. Micromammifères et biochronologie des formations néogènes du flanc sud du Haut-Atlas Marocain: implications biogéographiques, stratigraphiques et tectoniques. *African Geoscience Review*, 2:279–310.
- Bleefeld, A. R., and W. J. Bock. 2002. Unique anatomy of lagomorph calcaneus. *Acta Palaeontologica Polonica*, 47:181–183.
- Brandt, J. F. 1855. Beiträge zur nähern Kenntniss der Säugethiere russlands. *Mémoire de l'Académie Impériale des Sciences*, St. Petersburg, Physique, Mathématique et Naturalistique, Séries, 6–9:1–365.
- Brunet, M., A. Beauvilain, D. Billiou, H. Bocherens, J. R. Boisserie, L. De Bonis, P. Branger, A. Brunet, Y. Coppens, R. Daams, J. Dejax, C. Denys, P. Düringer, V. Eisenmann, F. Fanoné, P. Fronty, M. Gayet, D. Geraads, F. Guy, M. Kasser, G. Koufos, A. Likous, N. Lopez-Martinez, A. Louchart, L. Maclatchy, H. T. Makaye, B. Marandat, G. Mouchelin, C. Mourer-Chauviré, O. Otero, S. Peigné, P. Pelaez Campomanes, D. Pilbeam, J. C. Rage, D. De Ruiter, M. Schuster, J. Sudre, P. Tassy, P. Vignaud, L. Viriot, and A. Zazzo. 2000. Chad: discovery of a vertebrate fauna close to the Mio-Pliocene boundary. *Journal of Vertebrate Paleontology*, 20:205–209.
- Dawson, M. R. 1967. Lagomorph history and the stratigraphic record, p. 287–317. *In* C. Teichert, E. L. Yochelson, and R. C. Moore (eds.), *Essays in Paleontology and Stratigraphy: R. C. Moore Commemorative Volume*. University of Kansas Press, Lawrence.
- Dawson, M. R. 1981. Evolution of modern lagomorphs, p. 1–8. *In* K. Myers and C. D. MacInnes (eds.), *Proceedings of the World Lagomorph Conference held in Guelph, Ontario, August 1979*. University of Guelph, IUCN Species Survival Commission, and World Wildlife Fund, Canada.
- Dice, L. R. 1917. Systematic position of several American Tertiary lagomorphs. *University of California Department of Geology Bulletin*, 10:179–183.



- Dice, L. R. 1929. The phylogeny of the Leporidae, with description of a new genus. *Journal of Mammalogy*, 10:340–344.
- Dice, L. R. 1931. *Alilepus*, a new name to replace *Allolagus* Dice, preoccupied, and notes on several species of fossil hares. *Journal of Mammalogy*, 12:159–160.
- Dice, L. R. 1932. Some characteristics of the skull and skeleton of the fossil hare *Palaeolagus haydeni*. *Michigan Academy of Science, Arts and Letters*, 28:301–306.
- Dietrich, W. O. 1942. Ältestquartäre Säugetiere aus der südlichen Serengeti, Deutsch-Ostafrika. *Paläontographica*, 94A:43–133.
- Fischer de Waldheim, G. 1817. *Adversaria zoologica*. *Memoires de la Société Impériale des Naturalistes du Moscou*, 5:357–428.
- Gray, J. E. 1821. On the natural arrangement of vertebrate animals. *London Medical Repository*, 15:296–310.
- Grayson, D. K. 1984. *Quantitative Zooarchaeology: Topics in the Analysis of Archaeological Faunas*. Academic Press, Orlando. 202 p.
- Hibbard, C. W. 1963. The origin of the P3 pattern of *Sylvilagus*, *Caprolagus*, *Oryctolagus* and *Lepus*. *Journal of Mammalogy*, 44:1–15.
- Hill, A. 1999. The Baringo Basin, Kenya: from Bill Bishop to BPRP, p. 85–97. In P. Andrews and P. Banham (eds.), *Late Cenozoic Environments and Hominid Evolution: A Tribute to Bill Bishop*. Geological Society, London.
- Kingdon, J. 1974. *East African Mammals: An Atlas of Evolution in Africa, Volume II, Part B (Hares and Rodents)*. Academic Press, New York.
- Lavocat, R. 1978. Rodentia and Lagomorpha, p. 66–89. In V. J. Maglio and H. B. S. Cooke (eds.), *Evolution of African Mammals*. Harvard University Press, Cambridge.
- Lyman, R. L. 1994. Relative abundances of skeletal specimens and taphonomic analysis of vertebrate remains. *Palaaios*, 9:288–298.
- Matthee, C., B. Van Vuuren, D. Bell, and T. Robinson. 2004. A molecular supermatrix of the rabbits and hares (Leporidae) allows for the identification of five intercontinental exchanges during the Miocene. *Systematic Biology*, 53:433–447.
- MacInnes, D. C. 1953. *Fossil Mammals of Africa No. 6: The Miocene and Pleistocene Lagomorpha of East Africa*. British Museum (Natural History), London. 30 p.
- McKenna, M. C., and S. K. Bell. 1997. *Classification of Mammals above the Species Level*. Columbia University Press, New York. 631 p.
- Meng, J., Y. Hu, and C. Li. 2005. *Gobiolagus* (Lagomorpha, Mammalia) from Eocene Ula Usu, Inner Mongolia, and comments on Eocene lagomorphs of Asia. *Palaentologia Electronica*, 8:1–23.
- Nowak, R. M. 1991. *Walker's Mammals of the World*. Fifth edition. Johns Hopkins University Press, Baltimore. 1629 p.
- Patnaik, R. 2002. Pliocene Leporidae (Lagomorpha, Mammalia) from the upper Siwaliks of India: implications for phylogenetic relationships. *Journal of Vertebrate Paleontology*, 22:443–452.
- Pavao, B., and P. W. Stahl. 1999. Structural density assays of leporid skeletal elements with implications for taphonomic, actualistic, and archaeological research. *Journal of Archaeological Science*, 26:53–66.
- Qui, Z. 1987. The Neogene mammalian faunas of Ertemte and Harr Obo in Inner Mongolia (Nei Mongol), China. Ch. 6. Hares and pikas (Lagomorpha: Leporidae and Ochotonidae). *Senckenbergiana Lethaea*, 67:375–399.
- Qui, Z., D. Hen, G. Qi, and L. Yufen. 1985. A preliminary report on a micromammalian assemblage from the hominoid locality of Lufeng Co. Yunnan Province. *Acta Anthropologica Sinica*, 4:13–32.
- Schlosser, M. 1924. Tertiary vertebrates from Mongolia. *Palaentologia Sinica, Series C*, 1:1–132.
- Schott, W. B., G. L. Jepsen, and A. E. Wood. 1940. The mammalian fauna of the White River Oligocene. *Transactions of the American Philosophical Society, New Series*, 28:271–362.
- Shotwell, J. A. 1955. An approach to the paleoecology of mammals. *Ecology*, 36:327–337.
- Shotwell, J. A. 1958. Inter-community relationships in Hemphillian (mid-Pliocene) mammals. *Ecology*, 39:271–282.
- Smith, J. B., and P. Dodson. 2003. A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. *Journal of Vertebrate Paleontology*, 23:1–12.
- Stromer, E. 1926. Reste Land- und Süßwasser-bewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas, p. 107–153. In E. Kaiser (ed.), *Die Diamantwüste Südwestafrikas, Volume 2*. D. Reimer, Berlin.
- Szalay, F. S. 1985. Rodent and lagomorph morphotype adaptations, origins, and relationships: some postcranial attributes analyzed, p. 83–132. In W. P. Luckett and J.-L. Hartenburger (eds.), *Evolutionary Relationships Among Rodents: A Multidisciplinary Analysis*. Plenum Press, New York.
- Terry, R. C. 2004. Owl pellet taphonomy: a preliminary study of the post-regurgitation taphonomic history of pellets in a temperate forest. *Palaaios*, 19:497–506.
- Van Couvering, J. A., and J. A. Miller. 1969. Miocene stratigraphy and age determinations, Rusinga Island, Kenya. *Nature*, 221:628–632.
- Van Valen, L. 1964. A possible origin for rabbits. *Evolution*, 18:484–491.
- von den Driesch, A. 1976. A guide to the measurement of animal bones from archaeological sites. Peabody Museum of Archaeology and Ethnology, Peabody Museum Bulletin 1, 136 p.
- Voorhies, M. R., and C. L. Timperley. 1997. A new *Prontolagus* (Lagomorpha: Leporidae) and other leporids from the Valentine railway quarries (Barstovian, Nebraska), and the archaeolagine-leporine transition. *Journal of Vertebrate Paleontology*, 17:725–737.
- White, J. A. 1991. North American Leporinae (Mammalia: Lagomorpha) from Late Miocene (Clarendonian) to Latest Pliocene (Blancan). *Journal of Vertebrate Paleontology*, 11:67–89.
- Winkler, A. J. 2002. Neogene paleobiogeography and East African paleoenvironments: contributions from the Tugen Hills rodents and lagomorphs. *Journal of Human Evolution*, 42:237–256.
- Winkler, A. J. 2003. Rodents and lagomorphs from the Miocene and Pliocene of Lothagam, Northern Kenya, p. 169–198. In M. G. Leakey and J. M. Harris (eds.), *Lothagam: The Dawn of Humanity in Eastern Africa*. Columbia University Press, New York.